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**1975 PROGRESS REPORT**

**PRIMARY PRODUCTION AND CARBON ALLOCATION  
IN CREOSOTEBUSH:  
THE EFFECT OF LEAF AGE ON NET GAS EXCHANGE CAPACITY**

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## ABSTRACT

Measurements of net gas exchange rates of growth-chamber-grown individuals of creosotebush (*Larrea tridentata*) were made to determine the effect of leaf age on net gas exchange capacity. It was found that dark  $\text{CO}_2$  release and stomatal and cuticular resistances to  $\text{H}_2\text{O}$  and  $\text{CO}_2$  were not affected by leaf age. Net  $\text{CO}_2$  uptake in the light was reduced due to changes in processes other than  $\text{CO}_2$  transport from the air to the evaporating surfaces of the leaf mesophyll. It was also found that an increase in the rate of leaf senescence is correlated with an increase in the rate of new leaf production.

## INTRODUCTION

Creosotebush (*Larrea tridentata*) is one of the most widespread and successful species of the warm desert regions of North America. The success of this evergreen perennial has led to a great deal of interest in, and investigation of, its physiological adaptations to hot xeric conditions. Information from these investigations has recently been summarized and reviewed (Barbour et al., in press) but no attempt was made to integrate the information into a complete functional description of the physiological ecology of the species. Such an integration, in the form of a heuristic model of primary production and carbon allocation, has been undertaken (Reynolds and Cunningham, in prep.). This undertaking has revealed several critical gaps in our knowledge of factors and processes associated with production of *Larrea*. One of these was a lack of knowledge about what determines the rate of leaf senescence and the manner in which net photosynthesis and dark respiration are affected by leaf senescence.

There is some indication in the literature that the rate of senescence of mature leaves is closely associated with the production rate of new leaves. Periods of greatest leaf drop and litter accumulation under *Larrea* coincide with periods of maximum growth rate (Ludwig and Whitford, in press, Chew and Chew 1965). Burk (1970) showed that leaf retention time for *Larrea* was inversely proportional to the rate of new leaf production and that leaves normally remained on the plant for a period of 12 months but could be retained somewhat longer if no new leaves were being produced. The longest leaf retention time ever observed for *Larrea* (Chew and Chew 1965) is 15 to 18 months. Two possible causes for the close association of senescence rate and new leaf production have been suggested for other species; water stress, which suspended growth, also reduced the rate of physiological aging (Gates 1968, Ludlow and Ng 1974); shading, which would presumably result from new leaf production, hastens the rate of senescence and leaf abscission (Hopkinson 1966).

Research on species other than *Larrea* indicates that net photosynthesis decreases with leaf age. Leaves are most active metabolically at about the time of full expansion. Maximum photosynthesis rates progressively decline after full expansion as the leaf ages and is finally abscised (Hardwick et al. 1968, Larson and Gordon 1969, Ludlow and Wilson 1971). This decline is correlated with a decline of both chlorophyll and photosynthetic enzyme content (Šesták 1963, Woolhouse 1967) and a concomitant increase in leaf resistance to  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor fluxes (Slayter and Bierhuizen 1964, Ludlow and Wilson 1971).

This research was undertaken to determine if the rate of leaf senescence, and subsequent abscission, could be increased by increasing the rate of new leaf production, and to determine the relationship between leaf age and gas exchange capacity.

## MATERIALS AND METHODS

*Larrea* individuals (< 20-cm height) were transplanted from various areas in Dona Ana County, New Mexico, into gallon pots containing the soil in which they were growing. The potted plants were allowed to become established in a greenhouse and were subsequently transported to the Southeastern Plant Research Phytotron at Duke University, Durham, North Carolina. The seedlings were then barerooted and repotted in a sterilized, coarse gravel and vermiculite (50:50 by volume) mixture and allowed to reestablish in a controlled environment chamber. The chamber was kept on a 16:8 hr day/night photoperiod with  $550 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PhAR, provided by a combination of fluorescent and incandescent lamps. The temperature was 30-20 °C on a 16:8 hr day/night thermoperiod; relative humidity within the chamber varied from 40-10%. Plants were watered every other day, alternating with half-strength Hoagland's solution and deionized water. Under these conditions, the plants grew extremely well; within a month the seedlings had completely recovered from transplanting and we were able to begin the leaf senescence gas exchange studies.

All terminal vegetative buds were marked with a small spot of India ink and, one week later, the new terminal buds were again marked in a similar fashion. Most seedlings put on at least one (some two or three) pair(s) of leaves at each terminal node during that time. About every 10 days for the following two months, three seedlings were randomly selected to be used for that particular age-class gas exchange measurements. Leaves and stems beyond the later mark, as well as leaves below the earlier mark, were removed. This left one or two pairs of leaves, all of the same age class, on each branch to be measured.

Transpiration, photosynthesis and respiration were measured, using methods described in Šesták et al. (1971). The open gas-exchange system incorporated a Plexiglas measurement cuvette, a Beckman Infrared Gas Analyzer (Model 215B) and an EG&C Cambridge dew point hygrometer (Model 880-C1). All measurements were made at air temperatures between 28 and 30.5 °C, and at a dew point of the air stream entering the cuvette of 10-12 °C. Vapor pressure deficits in the cuvette varied from 14.03 to 21.63 mm Hg. The light source was a 300 W flood lamp

(G.E. Par 56/2 MFL) with 5 cm of a 15% copper sulfate solution to reduce the nonvisible component. Photosynthesis measurements were made at  $550 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PhAR as measured with a Lambda quantum sensor (LI-190SR).

Transpiration rates were calculated on a leaf-area basis as a function of the difference between the concentration of water vapor leaving and entering the measurement cuvette. The leaf diffusive resistance to water vapor ( $r'_1$  = stomatal and cuticular resistances) was estimated by dividing the water vapor concentration gradient between the leaf and the air ( $\Delta\text{H}_2\text{O}$ ) by the measured transpiration rate ( $F_{\text{H}_2\text{O}}$ ):

$$r'_1 = \Delta\text{H}_2\text{O}/F_{\text{H}_2\text{O}}$$

The water vapor concentration of the cuvette air was calculated from the dew point temperature of air leaving the cuvette. The water vapor concentration at the evaporating surfaces of the mesophyll was assumed to be that corresponding to the saturation vapor concentration at air temperature. The leaf diffusive resistance to  $\text{CO}_2$  ( $r_1$ ) was derived by multiplying the  $r'_1$  by the ratio of the diffusion coefficients of water vapor and  $\text{CO}_2$  in air ( $D_{\text{H}_2\text{O}}/D_{\text{CO}_2}$ ). We used the value 1.605 from Fuller et al. (1966, in Šesták et al. 1971). For a discussion of the problems and the possible inaccuracies of incorporating such a correction, see Jarman (1974). Boundary layer resistances were assumed to be insignificant, since the measurement cuvette was well stirred to maintain constant turbulence.

Net  $\text{CO}_2$  exchange rates were calculated as a function of the difference between the  $\text{CO}_2$  concentration entering and leaving the measurement cuvette ( $\Delta\text{CO}_2$ ). An independently measured rate of net  $\text{CO}_2$  release from stems, under identical conditions, was added to the measured exchange rates to obtain rates of net  $\text{CO}_2$  exchange for leaves alone. A residual resistance ( $r_r$ ) was equated to the  $\text{CO}_2$  concentration gradient between the  $\text{CO}_2$  reduction site, and the air within the measurement cuvette ( $\Delta\text{CO}_2$ ) was divided by the calculated  $\text{CO}_2$  flux rate ( $F_{\text{CO}_2}$ ) minus the calculated  $r_1$ :

$$r_r = (\Delta\text{CO}_2/F_{\text{CO}_2}) - r_1$$

The consequence of this calculation is that the term  $r_r$  includes biochemical processes involved in  $\text{CO}_2$  production and reduction represented as resistances to  $\text{CO}_2$  transfer, the actual resistances to  $\text{CO}_2$  transfer from the evaporating surfaces of the leaf mesophyll cells to the chloroplast reduction sites, and any real resistances to transfer between  $\text{CO}_2$  production and reduction sites within the leaf.

Since it was not possible to make all measurements of net  $\text{CO}_2$  exchange under exactly the same conditions of  $\text{CO}_2$  concentration and vapor pressure deficit, it was likely that some of the variation in net  $\text{CO}_2$  exchange rate was due to differences in  $\Delta\text{CO}_2$  and  $r_1$  rather than to effects of leaf age. Therefore, net  $\text{CO}_2$  exchange rates for standardized conditions of  $\Delta\text{CO}_2$  (315 vpm) and  $r_1$  ( $2\text{ s}\cdot\text{cm}^{-1}$ ) were calculated:

$$F_{\text{CO}_2} = \Delta\text{CO}_2/(r_r + r_1)$$

where  $F_{\text{CO}_2}$  is the net  $\text{CO}_2$  exchange rate in milligrams,  $\text{CO}_2\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$ ;  $\Delta\text{CO}_2$  is  $618\text{ mg}\cdot\text{cm}^{-3}$  at STP;  $r_1$  is  $2\text{ s}\cdot\text{cm}^{-1}$ ; and  $r_r$  is calculated as given above.  $F_{\text{CO}_2}$  was converted into  $\text{mg}\text{CO}_2\cdot\text{gdw}^{-1}\cdot\text{h}^{-1}$ , using the surface area of one side to dry weight ratio of  $170\text{ cm}^2\cdot\text{g}^{-1}$ . This was done so that the net  $\text{CO}_2$  exchange rate values reported here would be comparable with rates previously reported for *Larrea*. One-way analysis of variances and least significant differences were used to test for differences between the mean rates.

The average rate of new leaf production was estimated by harvesting five plants once every two weeks and obtaining dry weights of both leaves and stems produced before and since the initial marking of vegetative buds.

## RESULTS

The mean relative productivity (kg dry wt produced/kg standing dry wt) for these plants was 0.89 for the nine-week duration of the experiment; the net assimilation (kg dry wt produced/kg leaves) was 1.3. Assuming these plants could maintain these growth rates for a six-month growing season, which is the period of time *Larrea* is metabolically most active in the field (Chew and Chew 1965, Ludwig 1974), the relative productivity and net assimilation values would become 2.6 and 3.7, respectively.

The variability in the measured and calculated gas exchange parameters, as estimated from the standard deviations, was quite large. This variability most likely reflects real genetic variation among the sample plants rather than slight differences which might arise from leaf-age variation within a given age class since no statistically different values appear until leaves are at least 47 days old. In the 47-51 day age class, a significant ( $P < .05$ ) increase in  $r_r$  was observed. This increase was, of course, reflected in a decreased  $F_{\text{CO}_2}$ . The increase in  $r_r$  was also observed in the oldest (63-69 day) age class measured but not in the intermediate (53-59 day) age class;  $r_1$  did not show a change with leaf age. No significant differences were observed among the mean rates of dark  $\text{CO}_2$  efflux of any of the age classes. The experiment was terminated after 69 days because leaves older than 69 days were not retained on the plant (Table 1).

## DISCUSSION

Although the results presented herein are by no means conclusive, they do provide some insights into the original questions posed and give a starting point for continued research and modeling efforts. The first question was, can the rate of leaf senescence and the time of leaf abscission be assumed to be a function of the rate of new leaf production? The answer seems to be yes. As pointed out above, Burk (1970) showed that in the field, leaf retention time for *Larrea* was inversely proportional to the rate of new leaf production. He reported average leaf retention times of about 12 months. Working in a nearby area on comparable

**Table 1.** Net dark respiration ( $R$ ), leaf ( $r_l$ ) and residual ( $r_r$ ) resistances to  $\text{CO}_2$  flux and corrected net photosynthesis ( $F_{\text{CO}_2}$ ) rates for the six age classes. Each value is a mean of three replicate plants and is followed by  $\pm 1$  SD; values followed by different superscripts are significantly different ( $P < .05$ )

Leaf age Class (d)	$R$ (mg $\text{CO}_2 \cdot \text{g}$ $\text{dw}^{-1} \cdot \text{h}^{-1}$ )	$r_l$ ( $\text{s} \cdot \text{cm}^{-1}$ )	$r_r$ ( $\text{s} \cdot \text{cm}^{-1}$ )	$F_{\text{CO}_2}$ (mg $\text{CO}_2 \cdot \text{g}$ $\text{dw}^{-1} \cdot \text{h}^{-1}$ )
17-19	$3.72 \pm 1.00$	$1.87 \pm 0.55$	$70.86 \pm 23.50^a$	$4.56 \pm 1.47^a$
24-29	$3.64 \pm 2.36$	$2.33 \pm 0.96$	$109.60 \pm 98.55^a$	$4.33 \pm 2.58^a$
33-41	$2.90 \pm 0.41$	$0.88 \pm 0.15$	$66.04 \pm 15.36^a$	$4.82 \pm 1.25^a$
47-51	$3.55 \pm 0.82$	$3.00 \pm 0.29$	$505.74 \pm 76.18^b$	$0.42 \pm 0.37^b$
53-59	$3.17 \pm 0.70$	$15.81 \pm 13.36$	$164.54 \pm 83.86^a$	$1.44 \pm 1.47^a$
63-69	$5.00 \pm 1.10$	$5.62 \pm 4.23$	$543.05 \pm 173.30^b$	$0.63 \pm 0.24^b$
	n.s.	n.s.	1sd(.05) = 230.37	1sd(.05) = 3.37

shrubs, Ludwig (1974) reported a mean relative productivity for *Larrea* of 0.21 for a six-month growing season. In the present study, mean relative productivity was increased to 2.6 if extrapolated to six months and leaf retention time was decreased to only 69 days.

Our second objective was to ascertain the relationship between leaf age and gas exchange capacity. It seems clear from the results that, after the leaf is mature, leaf age has no detectable effect on the rate of dark  $\text{CO}_2$  release by leaves. Further, it appears that stomatal and cuticular resistances to  $\text{H}_2\text{O}$  and  $\text{CO}_2$  are not affected by leaf age once the leaf has fully expanded. Net  $\text{CO}_2$  uptake in the light is affected by leaf age following full expansion. In the present study, net  $\text{CO}_2$  uptake remained at the level obtained immediately following full expansion until after day 47. The leaves had all abscised by day 69. It is not clear from the present study whether reduced rates of net  $\text{CO}_2$  uptake can always be expected after approximately 47 days or whether the reduced rates occur only during the last 22 or so days of the leaves' existence. It would appear, however, that the latter is more likely since, in this study, leaf senescence was greatly accelerated over rates commonly observed in the field. We cannot say which of the many processes involved in the  $r_r$  term was responsible for the decreased net  $\text{CO}_2$  uptake rates. We did, however, notice a visible yellowing of leaves in the two age classes which exhibited increased values of  $r_r$ . Thus, a reduction in chlorophyll content and subsequent ability to provide reducing power may be among the possible causes.

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